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INTROGRESSION OF ALNUS SERRULATA AND ALNUS RUGOSA

FREDERIC L. STEELE

In the eighth edition of Gray's Manual of Botany, two species of alders in the subgenus Alnus are indicated as occurring in New Hampshire, each of which has a variety and several forms. The two species are distinguished as follows: *Alnus rugosa* (Du Roi) Spreng. has leaves with a rounded base, ovate or elliptical in shape with a tendency to be broadest below the middle, doubly-toothed leaf margin, strong veins on the green lower surface, prominent lenticels on the stems, and nutlets and bracts with a characteristic shape. Its variety *americana* (Regel) Fern. differs in having leaves glaucous rather than green underneath. *Alnus serrulata* (Ait.) Willd. has leaves with angled or cuneate base, obovate and broadest above the middle, a margin almost singly toothed, weak or vanishing veins on the green or glutinous lower surface, inconspicuous lenticels, and nutlets and bracts differing from *A. rugosa* in a way to be stated later. Its variety *subelliptica* Fern. has broader leaves, although still broadest above the middle, and a rounded leaf base.

The present study was started when the writer became interested in the northern limits of the ranges of these two species and their varieties in New England. *A. rugosa* var. *americana* is a well-marked variety occurring throughout northern New England and extending north to Labrador. Fernald (1945) states that this variety is decidedly more northern in range than var. *rugosa*. An investigation of the range of the latter from herbarium sheets presented some

difficulties. The question of whether leaves are glaucous or green can only be determined from mature leaves and in natural light. Under these conditions, if the observer has had some practice, the distinction is readily apparent. Many of the herbarium specimens were collected in April when there were no leaves, so that the distinction can not be made. In other cases, the specimens were mounted in such a way that it was possible to examine the lower surfaces of the leaves. Subsequent field observations indicate that the new leaves of var. *americana*, as they appear in June are green; by early July they become glaucous. Alder typically grows in swamps or open low land; when it grows in shady environments the leaves are thin and pale green with the glaucous character barely discernible. The material on some sheets that were labeled var. *rugosa* was of uncertain identity. Altered notations on many sheets indicated confusion of *A. serrulata* with *A. rugosa* var. *rugosa*.

In Tamworth, New Hampshire, A. *rugosa* var. *americana* is common in open moist habitats. There plants are quick to invade a poorly-drained hayfield and are also common along streams. *A. serrulata* is near its northern limit in Tamworth and is confined to shores of lakes and occasionally along edges of rocky streams. Some plants occur that can be referred to *A. rugosa* var. *rugosa*. These, however, although having green leaves which set them off from var. *americana* are not readily distinguishable from *A. serrulata*. As the scope of this investigation was broadened to include the whole state of New Hampshire, this situation was observed to be characteristic. It seemed probably that hybridization and introgression were going on between *A. rugosa* var. *americana* and *A. serrulata* producing a mixed assemblage of plants, some of which could be referred to var. *rugosa*.

To investigate this situation, it was decided to study populations and analyze them by pictorialized scatter diagrams of the type devised by Anderson (1949, 1952, 1953). Characters to be used were based on leaves, lenticels, and fruit. As there is considerable variation in leaves on sterile plants, especially on young shoots, only leaves on fruiting branches were used. Preferably these were collected after the middle

of July when the fruit was mature. An alder colony typically consists of a number of separate clumps of plants, which, judging from the variation that occurs, are clonally distinct, although it is possible that in some cases a new clump could arise from a rootstock. In a colony extending for a distance of two or three hundred feet, many plants may not fruit, so the sampling consisted of collecting branches from available fruiting plants that appeared to be separate. Leaves on fruiting branches are typically quite small. Where possible a branch was collected with at least one undamaged leaf six to eight centimeters in length. Lenticel type is significant, and, as collection of bark is difficult, the character of the lenticels was noted at the time. Notches were then cut on the branches in accordance with a standardized code; three notches indicating prominent lenticels, two indicating that some were indefinite, and one indicating the lenticels were indistinct.

Seven characters were scored including most of those used by Fernald in the eighth edition of Gray's Manual. The angle at the base of the leaf was measured on a 15° degree sector scale.

Single as opposed to double serration was determined by counting the major teeth on one leaf margin using certain "typical" leaves from well marked samples of the two species as standards for comparison.

The character of the lower surface of the leaves, ranging from glutinous to glaucous, was determined by examining the leaves in daylight and again comparing with standards. Usually the distinction between green and glaucous was obvious, but where the glaucous character could barely be discerned, the leaves were marked pale. Sometimes it appeared as if the leaves were glaucous because of disease.

To measure whether the leaf was broadest above or below the middle, it was placed on graph paper and the broadest point determined. The distance from this point to the midpoint of the leaf was divided by half the length of the leaf to form the "midratio". This was taken as positive if the broadest point was above the middle and negative if it was below.

Lenticels, especially on larger stems, are usually prominent in the case of *A. rugosa* var. *americana* and indistinct

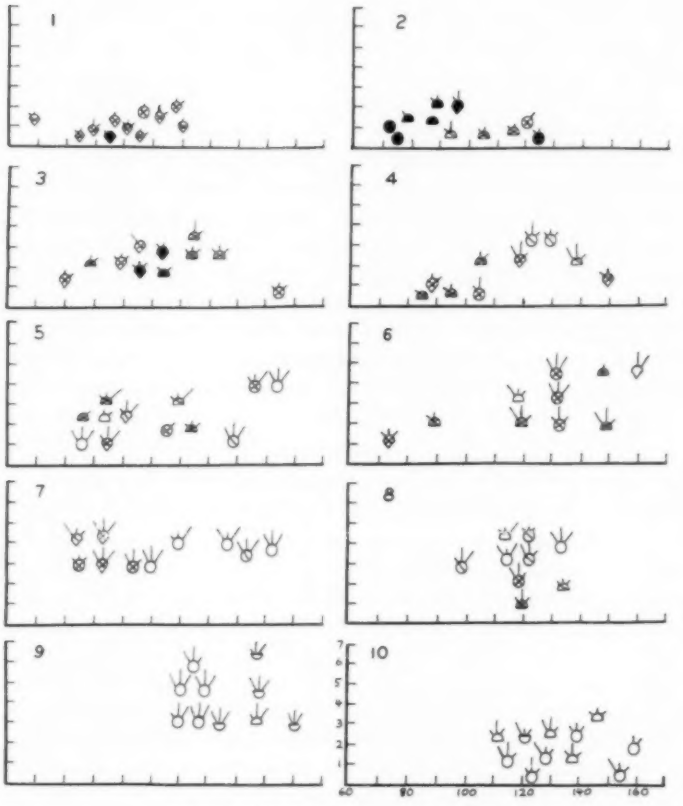
in the case of *A. serrulata*. The lenticel character was recorded at the time of collection as indicated above.

Veins on the lower surface were ranked as prominent, intermediate or vanishing. This character was somewhat variable, but well-marked trends were apparent. The leaves were compared with characteristic leaves of *A. serrulata* and of *A. rugosa* var. *americana* and rated according to which one of the two they most nearly approached.

Well developed nutlets and bracts of the two taxons seemed to be markedly different. The bracts of *A. serrulata* have a lower portion with straight narrow sides with the upper portion rather abruptly flaring; the bracts of *A. rugosa* var. *americana* have the lower portion with diverging sides, with the upper portion less distinct. Nutlets of var. *americana* tend to be rhombic with the top portion triangular. Nutlets of *A. serrulata* are obovate with prominent shoulders at the top. These differences become apparent when the fruit is mature; about the middle of July in New Hampshire. On the diagrams the fruit is labeled broad if the nutlets and bracts resemble var. *americana;* narrow if they resemble *A. serrulata.*

Some fifty populations were sampled from different areas of New Hampshire and northern Massachusetts, with an effort made to sample different environments. Then populations believed to be typical of the situation are shown in Figures 1 - 10. Following Hardin (1957), intermediates are labeled "species A" × "species B", while apparent back crosses are labeled as "species A" (× "species B") indicating that "species B" contributed the minority of the genes. Figure 1 from a swamp shows typical *A. serrulata.* Figure 2 from a lake shore shows *A. serrulata* near the northern limit of its range where much *A. rugosa* var. *americana* is present. It appears to be good *A. serrulata* but may not be genetically pure. Figure 3 from a swamp shows *A. serrulata*

FIG. 1-10. Pictorialized scatter diagrams showing introgression between *A. serrulata* and *A. rugosa* var. *americana*. All collections by the author. 1. *A. serrulata* (Boxford, Mass.). 2. *A. serrulata* (Tamworth, N. H.). 3. *A. serrulata* (× var. *americana*) (Hampton, N. H.). 4. *A. serrulata* (× var. *americana*) (Freedom, N. H.). 5. *A. serrulata* × var. *americana* (Hampton, N. H.). 6. *A. serrulata* × var. *americana* (Freedom, N. H.). 7. *A. rugosa* var. *americana* (× *A. serrulata*) (Tamworth, N. H.). 8. *A. rugosa* var. *americana* (× *A. serrulata*) (Milton, N. H.). 9. *A. rugosa* var. *americana* (Sandwich, N. H.). 10. *A. rugosa* var. *americana* (Ossipee, N. H.).



EXPLANATION OF SYMBOLS

ABSCISSA — MIDRATIO: +.2, +.1, 0, -.1, -.2

ANGLE AT BASE — LEAF COLOR: GLAUCOUS, PALE, GREEN, GLUTINOUS

ORDINATE — NUMBER OF TEETH

LENTICELS: PROMINENT, WEAK, VANISHING

VEINS: STRONG, WEAK, VANISHING

FRUIT: BROAD, INTERMEDIATE, NARROW

modified by genes from var. *americana* and contains three plants in the upper right of the diagram that could be called var. *rugosa*. Figure 4 from a sandy lake shore also shows modification of *A. serrulata* by genes from var. *americana*. In this case some of the plants might be referred to *A. serrulata* var. *subelliptica*. Figure 5 from a swamp and Figure 6 from a lake shore show populations about intermediate between *A. serrulata* and var. *americana*. Figure 7 and Figure 8 both from swamps show var. *americana* modified somewhat by *A. serrulata* and include plants that could be referred to var. *rugosa*. Figure 9 from a poorly drained field shows good var. *americana* unmodified by any *A. serrulata*. Figure 10 from the edge of an acid peat bog shows var. *americana* apparently modified by the acid environment. The leaves are smaller and the major teeth less prominent.

TABLE 1

TAMWORTH			FREEDOM		
Plant No.	Leaf angle	Width/length	Plant No.	Leaf angle	Width/length
1	75	.45	1	90	.65
2	75	.5	2	105	.6
3	90	.5	3	105	.7
4	90	.6	4	120	.6
5	90	.7	5	120	.75
6	105	.7	6	120	.8
7	120	.6	7	135	.7
8	120	.7	8	150	.8

These populations are apparently typical of the alder situation, judging from field studies in northern New England and herbarium studies for the whole area in eastern North America. *A. rugosa* var. *americana* is a distinct taxon with constant characteristics, especially in the northern part of its range where no *A. serrulata* is present. *A. serrulata* is a distinct species, with a range more southern than that of var. *americana*, extending north to north-central New Hampshire and central Maine. When the two taxa occupy the same area, introgression occurs producing intermediates, and plants that approach one or the other of the supposed parent. These intermediates do not seem to demand any particular hybridized environment, although they normally

occur in places that may be regarded as somewhat intermediate, and that have almost invariably been disturbed by man. Plants close to var. *americana* but green underneath could be referred to var. *rugosa;* however, these usually are variable and resemble *A. serrulata* in some respects.

The key characters that distinguish var. *subelliptica* from var. *serrulata* are leaves gradually rounded at base as opposed to cuneate or subacute, and broad leaves with a width-length ratio of .6 to .9 as opposed to narrower leaves with a ratio of .35 to .65. Width to length ratios were measured for a number of populations. Table 1 shows some typical results. Var. *subelliptica* appears to be one extreme of the normal variation of *A. serrulata* populations, although in some cases these populations may be modified by gene flow from var. *americana*. There is no indication that var. *subelliptica* is a geographic variety.

There are various named forms of both species and varieties, some of them depending on pubescence of lower surfaces of leaves. Many populations of both species had leaves varying from glabrous to varying degrees of pubescence. *A. serrulata* forma *nanella* is described as a dwarf shrub with small leaves and aments. Alders growing in adverse environments, such as peat bogs or silty shores of rivers are frequently stunted. *A. serrulata* forma *emarginata* has emarginate leaves. It is not infrequent to find an alder with some of the leaves emarginate.

In conclusion it appears that in the subgenus Alnus, in the northeast, the two good native taxa are *A. serrulata* and *A. rugosa* var. *americana*. The latter can readily be distinguished by the glaucous character of the lower surface of the mature leaves. Any plant with this trait, if not diseased, will possess the other characteristics of the taxon. Plants with deep green or glutinous leaves and cuneate leaf bases will possess the specific characters of *A. serrulata*. These two taxa hybridize and backcross frequently, the resulting gene exchange producing a variable assemblage of plants including some intermediates that would be referred to *A. rugosa* var. *rugosa*.

ACKNOWLEDGEMENTS. During the course of this study the author has been greatly helped by the encouragement and criticism of Dr. A. R. Hodgdon, Durham, N. H. Extensive use was made of the Herbarium of the New England Botanical Club. Dr. R. C. Rollins kindly allowed me to use the Gray Herbarium at Harvard University. — ST. MARY'S -IN-THE-MOUNTAINS, LITTLETON, N. H.

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SOME NEW OR OTHERWISE INTERESTING REPORTS OF LILIACEAE FROM THE SOUTHEASTERN STATES[1]

EDWARD T. BROWNE, JR.

Several interesting plants in the Liliaceae have been found as a consequence of field work in the southeast. As might be expected, this family is one of the best represented ones in our herbaria, but it is still incompletely known.

One of these collections consisted of several specimens of *Aletris* collected by Dr. W. H. Duncan of the University of Georgia. Dr. Duncan found both white- and yellow-flowered *Aletris* plants growing in approximately equal numbers in the same population in Chatham Co., Georgia, and they appeared at first to be plants of *A. farinosa* L. and *A. lutea* Small, respectively.

Since perianth color and shape are the two most important characteristics for specific separation in the North American species of *Aletris*, the identifications appeared to be obvious. However, upon closer examination, it was discovered that in neither of these types was there semi-epigyny, one of the

[1]This paper was supported in part by grants from the Faculty Research Fund, Graduate School, University of Kentucky.

most outstanding floral characteristics of *A. farinosa*. Microscopic and macroscopic examination of leaves of these plants revealed that both exhibited the narrow hyaline margin which is typical of the leaves of *A. lutea*. From this information it has been concluded that this population consists of typical *A. lutea* and white-flowered individuals of *A. lutea*. Thus, the latter are hereby designated as a new color form as follows:

Aletris lutea Small, forma **albiflora** E. T. Browne, Jr., f. nov. Forma nova floribus albis.[2]

This new form differs from the typical form only in flower color. The perianth tube is cylindric with recurved tepals.

This is the first reported color form of North American *Aletris* species. Because of the importance attached to flower color in the identification to species of plants in this genus, careful review of the specimens presently deposited in herbaria will be necessary for proper determination. It is significant that *A. farinosa* has apparently not been collected in the Lower Coastal Plain of Georgia, and although these specimens are obviously those of a population of *A. lutea*, this latter species has not turned up in the collections made in connection with the Flora of the Carolinas Project which includes a geographic area in part not very far removed from this Chatham County locality (H. E. Ahles, personal communication).

Specimens cited: GEORGIA. Chatham Co. Open area, low ground at edge of cypress stand, 15.3 mi. W4°S of Savannah City Hall. Coastal Plain Province. *W. H. Duncan, 20982.* 13 June 1958.

The holotype has been retained in the Herbarium of the University of Georgia. Dr. Duncan has presented an isotype and a specimen of the typical form *(Duncan, 20980)* to the Herbarium of the University of Kentucky.

Another *Aletris* variant was observed in mixed populations of *A. lutea* and *A. obovata* Nash. These individuals had cream-colored flowers instead of yellow and white flowers as in *A. lutea* and *A. obovata*, respectively. The perianth tips of *A. lutea* are recurved while those of *A. obovata* are not. This variant is characterized by a perianth of intermediate color

[2]Appreciation is expressed to Dr. W. L. Carr, Department of Ancient Languages, University of Kentucky, for the Latin diagnoses in this paper.

and shape but without recurved perianth tips. Since these plants were observed only in mixed populations of the two species previously referred to, or in the near vicinity of populations of both species, the variant individuals are strongly suggestive of probable interspecific hybridization between these two species. Therefore, this putative hybrid is designated in the following way:

Aletris × Tottenii E. T. Browne, Jr., hybr. nov. *Aletris × Tottenii*, hybrida naturalis nova inter *A. luteam* et *A. obovatam*. Herbae mediae inter species parentales. Folia basalibus rosettis, hyalino margine, colore sulfureo-viridi, lanceolata, 52-96.5 mm. longa et 6.2-11.5 mm. lata. Calami et bracteati racemi 5.1-7.7 dm. alti cum multis floribus. Flores horizontales aut prope horizontales, colore aliquantum vario inter ochroleucum et ebureum (cream-colored). Ultimae partes perianthorum non recurvatae. Forma et magnitudo tubae perianthi aliquantum variae inter species parentales.

Plants intermediate between the parental species. Perianth segment tips not recurved (perhaps appearing so in pressed material).

Specimens examined: GEORGIA — Berrien Co. Highway right of way, Ga. 135, 1.3 mi. S of Berrien-Atkinson Co. line. Flowers cream color. May 7, 1960. *Elizabeth M. and E. T. Browne, Jr. 2516;* Colquitt Co. Highway right of way, US 319, 0.1 mi. N of Colquitt-Thomas Co. line. Flowers varying in color from light to deep cream color in the three specimens collected at this locality. May 8, 1960. *Elizabeth M. and E. T. Browne, Jr. 2524.* (holotype, KY); Cook Co. Highway right of way, Ga. 76, 5.3 mi. N of Cook-Brooks Co. line. Flowers light cream color. May 7, 1960. *Elizabeth M. and E. T. Browne, Jr. 2519.*

This putative hybrid was first reported in the literature by Harper (1905, 1906). He did not name the hybrid, but he did suggest its hybrid nature. Since in form of the perianth there is a somewhat closer resemblance to *A. obovata* than to *A. lutea*, some botanists might suggest that this variant constitutes only a color form of *A. obovata*. However, this suggestion is not tenable since these plants are found only in mixed populations of *A. lutea* and *A. obovata* or in the near vicinity of pure populations of both species. In addition, while these species usually occur in separate populations, especially along highways they have become mixed presumably as the result of highway maintenance operations, and this fact has undoubtedly contributed to their hybridization. Apparently, the parental species are not highly interfertile since there are very few of the putative

hybrids to begin with, and there is no evidence to indicate that offspring are produced beyond the F_1 generation.

The putative hybrid, *Aletris* × *Tottenii*, has been named for Dr. Henry Roland Totten, Professor of Botany in the University of North Carolina, Chapel Hill.

A double-flowered form of *Lilium superbum* L. was found near Oakland, Garrett Co., Maryland, in 1954. Bulbs of this form were transplanted to Chapel Hill and Elon College, N. C., where they flowered the two following years. While this form is not as attractive as the typical form, it is worthy of mention since this is the first reported double-flowered variation of a native species of *Lilium*. As such, this new form is being designated as:

Lilium superbum L., forma **plenum** E. T. Browne, Jr., f. nov. Forma nova cum tepalis plenis.

In this double-flowered form some of the stamens have been changed entirely or in part to tepals. The pistil is unaffected, and plants of this form could, therefore, be fertile. This collection represents the only occurrence of this variation among several thousand individuals of this species observed at this locality and elsewhere by the writer in Maryland, Virginia, West Virginia, North Carolina and Kentucky.

Specimens cited: MARYLAND. Garrett Co. Near Oakland. July 6, 1954. *Edward T. Browne, Jr., s.n.* (holotype, NCU; isotype, KY).

A student in an undergraduate botany class has discovered a population of *Trillium pusillum* Michx. in Casey Co., Kentucky. This is the first report of this species from the state. The determination has been verified by Stanley J. Smith, New York State Museum, Albany. Mr. Smith writes that this species has been previously reported from only four other widely separated localities in the United States: the Chesapeake Bay region, the Carolinas, the Ozarks and the Sabine River region of Texas, and he feels that the Kentucky specimens are nearest those from the Ozarks, *T. pusillum* Michx., var. *ozarkanum* (Palmer and Steyerm.) Steyerm. (Stanley J. Smith, personal communication).

Specimen cited. KENTUCKY. Casey Co. Pricetown, 4 mi. S of Liberty and E of US 127. Open field, rocky soil. April 28, 1961. *Glenn W. Murphy, 92.* (KY).

In connection with a taxonomic monograph of the Liliaceae of Kentucky which the writer is undertaking preliminary to biosystematic studies in this family, several species

have been found in herbaria or collected which have apparently not been reported for the state. Among these species is *Smilacina stellata* (L.) Desf. which would be expected to occur in Kentucky on the basis of its distribution in adjacent states, but, according to the distribution given by Small (1933) and Fernald (1950) and the smaller works of McFarland (1942) and Braun (1943), the species does not occur in Kentucky. However, *S. stellata* is reported from Kentucky (as *Vagnera stellata*) in the second edition of Britton and Brown (1913), but it is not reported for Kentucky in the New Britton and Brown (Gleason, 1952). Although Galway (1945) indicates the presence of *S. stellata* in Kentucky on the distribution map of this species in her monograph of North American *Smilacina*, she does not cite any specimens from the state.

Specimens cited: KENTUCKY. Jefferson Co. In sylvis. Louisville, Ky. *C. Mohr, 2921.* (Annotated by Desma H. Galway, 1939; MO, 147191); Kentucky. (No county or other data given). 1840. *C. Short, s.n.* (GH).

Xerophyllum might be expected to occur in Kentucky based on its distribution in adjacent states. However, this writer has not collected any specimens of this genus in Kentucky although a considerable effort has been made to locate plants. One collection apparently made in the state has come to the writer's attention nevertheless. If the validity of this collection can be established, it will constitute a new state record since this genus is not given for Kentucky in any of the manuals, floras or papers of more limited extent.

On the sheet in question is an annotation label of K. J. Stone who has written: "*X. tenax* (Pursh) Nutt. Locality highly doubtful." *X. tenax* has a reported range from Wyoming to British Columbia and California (Abrams, 1940). On the other hand, *X. asphodeloides* (L.) Nutt. has a range from "Virginia to Georgia and Tennessee" (Fernald, 1950), and this fact would support the identification of this specimen as *X. asphodeloides*. In addition, in floral characteristics this specimen most closely approximates the latter species. Fernald (1950) points out that *X. asphodeloides*

also occurs on "sandy pinelands, New Jersey, Delaware and North Carolina." Situations similar to these, though of not the same geological origin, occur in various areas of west-central and western Kentucky, and it is not unlikely, therefore, that this specimen was collected in one of these places. It should be further pointed out that the place of collection, Bowling Green, is situated in the Barrens area of Kentucky.

Specimen cited: KENTUCKY. (Warren Co.) Bowling Green. 1903. *Sadie F. Price, s.n.* (MO).

Intensive field work has been under way in an attempt to relocate this species as well as *Smilacina stellata* in Kentucky. At this writing these efforts have so far proved futile. In regard to *Xerophyllum*, much acreage of the Barrens has been put into pasture and cultivation. It may be that both of these species, which in recent times have not been abundant, are now extinct or nearing this status in the state.

Fernald (1950) indicates that *Yucca Smalliana* Fern. is probably only introduced and escaping north of North Carolina and Tennessee. This species occurs widely in Kentucky, and in some instances, it is freely reproducing and persisting around abandoned homesites. Braun (1943) writes that *Y. filamentosa* L. is "occasional along roadsides and railroad tracks". The writer has not seen any specimens of *Y. filamentosa* in a natural state anywhere in Kentucky, and presumably it is actually *Y. Smalliana* to which this reference applies if these species are distinct. This latter species is not recorded by Fernald (1950), Gleason (1952), Small (1933), McFarland (1942) or Braun (1943) as occurring in Kentucky. While perhaps it may not be native to the state, *Y. Smalliana* should certainly be considered a member of the vascular flora of this area.

Specimens cited: KENTUCKY. Barren Co. US 68, 0.8 mi. E of Barren-Warren Co. line. July 15, 1961. *Elizabeth M. and E. T. Browne, Jr. 4570;* Boone Co. US 25, 5.2 mi. N of Boone-Kenton Co. line. Open field between highway and Southern Rwy. tracks. Scattered plants. July 8, 1961. *Elizabeth M. and E. T. Browne, Jr. 4469;* Boyle Co. US 68, just S of Boyle-Mercer Co. line at bridge. July 15, 1961. *Elizabeth M. and E. T. Browne, Jr. 4597;* Carter Co. Dry roadside cut about ½ mi. E of bridge over Tygarts Creek, Ky. 182. July 1, 1961. *Elizabeth M. and E. T. Browne, Jr. with J. C. Warden. 4421;* Edmonson Co. Ky. 259, 6.9

mi. E of junct. Ky. 185 and Ky. 70. Dry roadside bank. July 16, 1961. *Elizabeth M. and E. T. Browne, Jr. 4598;* Fayette Co. Lexington. Persisting and spreading after cultivation on vacant tract of land across the Southern Rwy. tracks from the passenger station near S. Broadway. July 6, 1961. *Elizabeth M. and E. T. Browne, Jr. 4460;* Grant Co. US 25, 6.8 mi. N of Grant-Scott Co. line. Open dry hillside. Plants of all ages. Very abundant. July 8, 1961. *Elizabeth M. and E. T. Browne, Jr. 4466;* Mercer Co. US 68, 11.3 mi. S of Mercer-Jessamine Co. line. Roadside. July 15, 1961. *Elizabeth M. and E. T. Browne, Jr. 4504;* Scott Co. US 25, 5.4 mi. N of Scott-Fayette Co. line. Open roadside. July 8, 1961. *Elizabeth M. and E. T. Browne, Jr. 4462;* Woodford Co. US 421, 3.6 mi. S of Woodford-Franklin Co. line. Steep road fill. Several plants in row as if planted. July 9, 1961. *Elizabeth M. and E. T. Browne, Jr. 4496.*

Allium ampeloprasum L. has been collected in three counties of west-central Kentucky. In each instance, these plants were found growing without cultivation apparently having originated from this source. As this species has not been previously reported from Kentucky, its mention here is justified. Undoubtedly, there are other localities in the state, other than those cited below, where this species is naturalized, but no other reports are available from elsewhere. As far as this writer is able to determine, this is apparently the first report of the occurrence of the typical variety of *A. ampeloprasum* in the United States as an escape (Small, 1933; Fernald, 1950; Gleason, 1952) since Fernald describes var. *atroviolaceum* (Boiss.) Regel as having "deep purple" flowers and Gleason, giving no varietal status to this, describes the flowers as "purple-red". The flowers of my collections were of several stages of development, and their color was light lavender becoming slightly darker upon drying.

Specimens cited: KENTUCKY. Butler Co. Ky. 185, 6.2 mi. N of ferry over Green River. Wet road cut. July 16, 1961. *Elizabeth M. and E. T. Browne, Jr. 4595;* Edmonson Co. Ky. 259, 6.9 mi. E of junct. Ky. 185 and Ky. 70. Dry roadside bank. July 16, 1961. *Elizabeth M. and E. T. Browne, Jr. 4599;* Warren Co. Ky. 67, 3.2 mi. E of junct. Ky. 67 and Ky. 263. Open roadside. July 16, 1961. *Elizabeth M. and E. T. Browne, Jr. 4591.*

The writer wishes to express his appreciation to the curators of the Gray Herbarium, the Herbarium of the Missouri Botanical Garden and the Herbarium of the University of North Carolina for permitting examination of specimens referred to herein. Dr. Herbert P. Riley has

kindly read the manuscript. — UNIVERSITY OF KENTUCKY, LEXINGTON, KENTUCKY.

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HYBRID ASPENS IN THE LOWER PENINSULA OF MICHIGAN[1]

BURTON V. BARNES[2]

INTRODUCTION

One explanation for the polymorphism and diversity found in the aspens, *Populus tremuloides* Michaux and *P. grandidentata* Michx., is an exchange of genes between these species through hybridization and backcrossing. Anderson (1949) and others have demonstrated the importance of introgression as a vital force in evolution. In a study of the natural variation and clonal development of the aspens in the Lower Peninsula of Michigan I searched for hybrids on two research sites on forest land of the University of Michi-

[1]Information from the author's dissertation submitted in partial fulfillment of the requirements of the degree of Doctor of Philosophy at the University of Michigan, Ann Arbor.

[2]Research Forester, Intermountain Forest and Range Experiment Station, Forest Service, U. S. Dept. of Agriculture, stationed at Northern Idaho Forest Genetics Center, Moscow, Idaho.

gan Biological Station, near Pellston, Michigan, and in other parts of Lower Michigan.[3] In this paper I shall list and describe aspen hybrids and putative introgressants discovered in the Lower Peninsula of Michigan and shall discuss briefly the ubiquity of the *P. grandidentata* × *P. tremuloides* hybrid in southeastern Michigan as compared with its apparent rarity in the northernmost part of Lower Michigan.

HYBRIDS AND INTROGRESSANTS

POPULUS GRANDIDENTATA × TREMULOIDES

A hybrid between *P. grandidentata* and *P. tremuloides* was first reported and described by Victorin (1930). Heimburger (1936) produced hybrid plants by crossing the two species. He reported a scarcity of natural *grandidentata-tremuloides* hybrids and said this might be explained by the fact that "*P. tremuloides* flowers about a week to ten days before *P. grandidentata* in nature." Pauley (1956) reported that *P. tremuloides* flowered from 10 to 14 days before *P. grandidentata* and stated that the hybrids were not infrequent in central and eastern Massachusetts. He had observed scattered hybrid individuals and hybrid swarms as well as what were presumed to be F_2 plants or backcrosses to one of the parents.

In April 1956 I discovered one hybrid clone on an abandoned field in Section 17, T. 10 N., R. 6 E., Saginaw County, Michigan. This hybrid was tentatively identified on the basis of the scattered hairs that were found on the terminal and lateral bud scales. Fallen leaves collected at the base of several trees in the group closely resembled the hybrid leaves illustrated by Pauley (1956).

A second hybrid was discovered in October 1957 on the forest land of the University of Michigan Biological Station (NW1/2, Section 25, T. 37 N., R. 4 W., Emmet County). The 13 living ramets of this clone were severely damaged by hypoxylon canker and were apparently unable to compete successfully with vigorous neighboring clones of quaking and bigtooth aspen. In August 1958 Dr. Warren H. Wagner,

[3]Barnes, Burton V. 1959. Natural variation and clonal development of *Populus tremuloides* and *P. grandidentata* in Northern Lower Michigan. 334 pp. Unpublished.

Jr., discovered a hybrid swarm in Monroe County. Consequently, in the fall of 1958 a more intensive search for hybrids was directed in southeastern Michigan. Thirty hybrid clones and putative introgressants were discovered in eight 3- to 8-hour trips. Many more hybrid clones could be located by systematic search in southeastern Michigan. Dr. Wagner located five additional clones in 1960. Hybrid clones have now been located in 10 counties of Michigan's lower peninsula. Location of these hybrid clones and putative introgressants is shown in the Appendix. Specimens of these will be deposited in the University of Michigan Herbarium.

Hybrids are typical in many localities in southeastern Michigan where the parent species occur. The number of hybrid clones is estimated at from 1 to 5 percent of those present in the localities observed. On the University of Michigan Biological Station land, however, the frequency is much lower, and this seems to be true for the entire Douglas Lakes area of the northern tip of the Lower Peninsula.

The apparent abundance of the hybrid in Lower Michigan may be due to several factors. The difference in flowering time between bigtooth and quaking aspen may not be as great as one might suspect. I can offer no proof, however, that this barrier is stronger in northern Michigan than in southeastern Michigan. I did observe numerous receptive female flowers on several *P. tremuloides* clones near Pellston, Michigan, at the time when *P. grandidentata* pollen was being discharged. These flowers were usually located at the base or tip of a catkin and represent an intraclonal lag in flowering. Einspahr and Joranson (1960) reported a somewhat similar intraclonal lag in flowering for seven aspen clones when their flower buds were forced to develop in the greenhouse. This intraclonal lag was apparently verified on only one tree under natural conditions. This developmental phenomenon may be closely related to the early-late leaf situation described by Critchfield (1960). Late flowering may be largely restricted to greenhouse conditions because not all flower buds may be in the same developmental stage when branches are collected 4 to 6 weeks before normal flowering time.

While intraclonal variation might explain the source of receptive female *P. tremuloides* flowers, there are at least two other explanations. Pauley (1956) pointed out that in areas of temperature inversion the flowering of female *P. tremuloides* clones may be retarded until it corresponds with the flowering time of neighboring *P. grandidentata* clones. Recognizing the wide range in the variability of both species, interclonal differences in flowering time might also account for pollination of *P. tremuloides* flowers by *P. grandidentata*.

Establishment of aspen seedlings is extremely difficult *(ibid.)*. This may be the reason why the hybrid is apparently much more abundant in southeastern Michigan than in the northern tip of the Lower Peninsula. In southeastern Michigan many hybrid clones were discovered in abandoned fields or along the edge of cultivated fields where they bordered a woodlot. There appears to be more repeated disturbance, primarily by cultivation, in southeastern Michigan than on University of Michigan Biological Station property and surrounding areas. More disturbance, coupled with more fertile soil and a somewhat more moderate climate in southeastern Michigan, probably means that the establishment of seedlings is easier.

Most ramets of the hybrid clones were not more than 2 or 3 inches in diameter at breast height and were probably younger than 20 years in age. Leaf samples from 25 of the hybrid clones were measured and examined in detail.[4] In general, the size of the hybrid leaves is intermediate between that of the parent species. The leaf shape of the hybrid clones varies as much as that within either of the parent species. To illustrate part of the variation among hybrid clones, two leaves typical of eight hybrid clones and typical leaves of the parent species are pictured in Fig. 1.

INTROGRESSION

Introgression, the flow of genes from one species into another through repeated backcrossing to either parent, has

[4]At least 50 leaves from each hybrid clone were measured to obtain the mean blade width, blade length, and petiole length. The number of teeth along both margins of at least 30 leaves of each clone was counted.

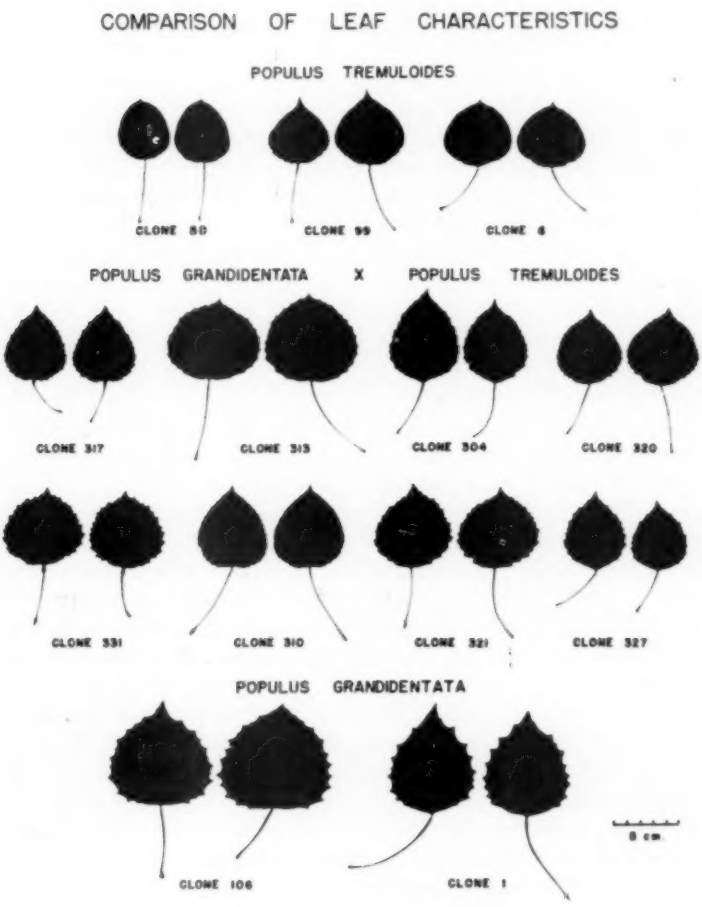


Figure 1

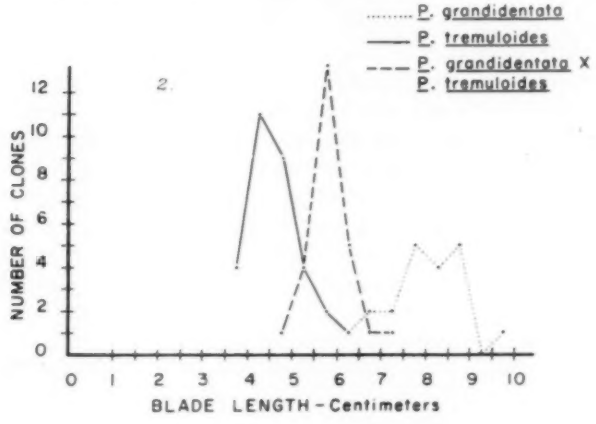
Comparison of leaf characteristics of *P. tremuloides*, *P. grandidentata*, and hybrids.

been described in *Acer* (Desmarais, 1952), *Quercus* (Cooperrider, 1957), and in several other plant genera (Anderson, 1949, 1953; Stebbins, 1950). A few hybrids collected in southeastern Michigan closely resemble *P. tremuloides*, yet have several characteristics of *P. grandidentata*. A series of frequency polygons illustrates leaf differences between the hybrids and the parent species (Figs. 2, 3, 4, 5). Since leaf specimens were not collected from the parents in southeastern Michigan, data from the aspen clones studied intensively in the forest of the University of Michigan Biological Station were used (Barnes, 1959). The hybrid clones are more nearly like *P. tremuloides* in respect to blade width, blade length, and petiole length. The number of teeth per leaf side, however, corresponds more closely to *P. grandidentata*. Of the four characters illustrating the intermediacy of the hybrid clones, the number of teeth per leaf side and the blade length are the most explicit quantitative characters separating hybrids from the parent species.

Hairiness of the terminal and lateral bud is one of the most striking differences between *P. tremuloides* and *P. grandidentata*. This character, however, lends itself less easily to quantification than the four leaf attributes. Anderson (1957), with a semigraphical method, used four of the more distinct features to characterize the differences among clones of the hybrids and parent species (Fig. 6). The hybrids are intermediate between the two parents, but they resemble *P. tremuloides* more closely than *P. grandidentata*. Three of the putative hybrid clones are suspected as being introgressants or backcrosses (clones 310, 317, and 333).

Without additional study and analysis of the parent and hybrid populations in southeastern Michigan, one can report only that the leaf characteristics of several hybrid clones closely resemble *P. tremuloides*. Usually, F_1 hybrids between distinct species are uniform in their characteristics, while segregates appear in the second and following generations (Anderson, 1949). However, the variation within both parents is so diverse and as yet only so summarily described, that F_1 plants seeming to resemble *P. tremuloides* in one, two, or more characteristics might be expected in the F_1 generation.

Sympatric introgression may occur between two distinct species that are ecologically or physiologically separated.


P. grandidentata
P. tremuloides
P. grandidentata X P. tremuloides
2.
NUMBER OF CLONES
0 2 4 6 8 10 12
0 1 2 3 4 5 6 7 8 9 10
BLADE LENGTH - Centimeters

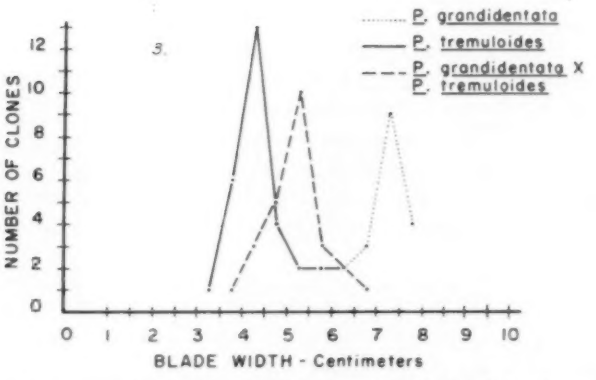

P. grandidentata
P. tremuloides
P. grandidentata X P. tremuloides
3.
NUMBER OF CLONES
0 2 4 6 8 10 12
0 1 2 3 4 5 6 7 8 9 10
BLADE WIDTH - Centimeters

FIG. 2. Frequency polygons illustrating differences in blade length for clones of the hybrid and the parent species.

FIG. 3. Frequency polygons illustrating differences in blade width for clones of the hybrid and the parent species.

Anderson (1948, 1949) pointed out that where the species are separated by habitat requirements, only when the "habitat is hybridized" can the F_1 hybrids find an ecological condition suitable for establishment and survival. In succeeding

generations, according to Anderson (1949), the hybrids segregate but the habitat usually does not. Thus, hybrid plants possessing about the same habitat requirements of either of the parent species, i.e. backcrosses to either parent, are favored over F_2 or successive generation segregates. *P. tremuloides* and *P. grandidentata*, however, are not isolated ecologically by their habitat requirements. The habitat of *P. tremuloides* overlaps that of *P. grandidentata*, and both species are frequently growing together on the same site. Therefore, disturbance by man or natural agents, is probably more important as a prerequisite to seedling establishment than "hybridizing the habitat." Thus, it is probable that in southeastern Michigan, F_1 and F_2 hybrids, as well as introgressants, would be about equally fitted for a given habitat that is suitable for both parents.

The variability of the parental species, *P. tremuloides* and *P. grandidentata*, may be due to multiple alleles for genes in the gene pool, mutation, drift, and introgression. Without further analysis it is difficult to say what combination of these factors is responsible for the polymorphism exhibited by the two species.

POPULUS ALBA × TREMULOIDES

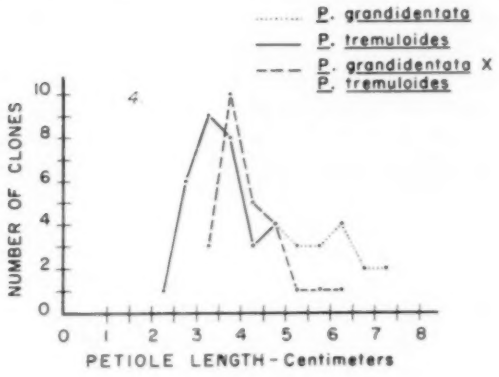
Two individuals of the *P. alba* × *tremuloides* hybrid were discovered in the Lower Peninsula. One clone was located at the edge of an abandoned field near the juncture of Woods Road and Highway M-18 (SE1/4, SE 1/4, Section 23, T. 23 N., R. 2 W., Gladwin County. The form of this tree resembles that of *P. tremuloides* rather than *P. alba* trees in Lower Michigan.

A second *P. alba* × *tremuloides* hybrid was discovered along the Deckerville Road, S1/2, Section 30, T. 13 N., R. 10 E., Tuscola County. This hybrid was recognized by its extremely shiny green leaves and its silvery bark.

P. alba × *P. tremuloides* hybrids were reported in Canada by Heimburger (1936) and Peto (1938). According to Peto, the *P. alba* × *tremuloides* hybrid was not as frequent as the *alba* × *grandidentata* hybrid in the vicinity of Ottawa, Canada.

The leaves of the *P. alba* × *tremuloides* hybrid are inter-

mediate in shape and serration between the parents. *P. alba* leaves are palmately lobed and tomentose on the undersurface. The margin of *P. alba* leaves is irregularly and shallowly serrate. The leaves of the hybrid are not lobed but are irregularly toothed. The teeth of the hybrid leaves resemble



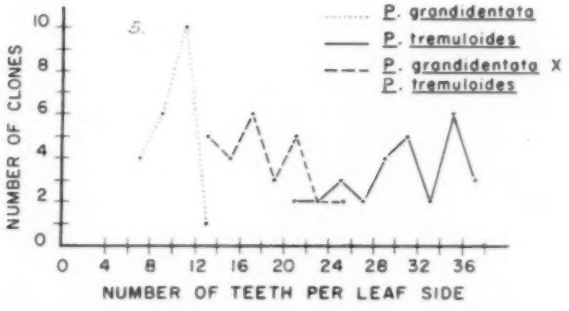

P. grandidentata
P. tremuloides
P. grandidentata X P. tremuloides
5.
NUMBER OF CLONES
0 4 8 12 16 20 24 28 32 36
NUMBER OF TEETH PER LEAF SIDE

FIG. 4. Frequency polygons illustrating differences in petiole length for clones of the hybrid and the parent species.

FIG. 5. Frequency polygons illustrating differences in number of teeth per leaf side for clones of the hybrid and the parent species.

those of *P. tremuloides* more than those of *P. alba*. The numbers of teeth per leaf side for the Gladwin and Tuscola County hybrids were 14.6 and 15.1, respectively. The under-

side of the immature leaves of the hybrid is moderately tomentose and becomes glabrous as the leaves mature.

Buds of the hybrids were covered with a tomentum that was not as dense as the tomentum on buds of *P. alba*. The immature shoots were also covered with a moderate amount of tomentum that did not entirely disappear from the new shoots during their initial year. The bark of the hybrid had many diamond-shaped cracks — a typical characteristic of *P. alba* trees of the same size. The bark was rougher in texture and more silvery-white in color than bark of typical sapling or pole-size trees of *P. tremuloides*.

Catkins collected from the hybrid in Gladwin County were predominantly male, but some female flowers were discov-

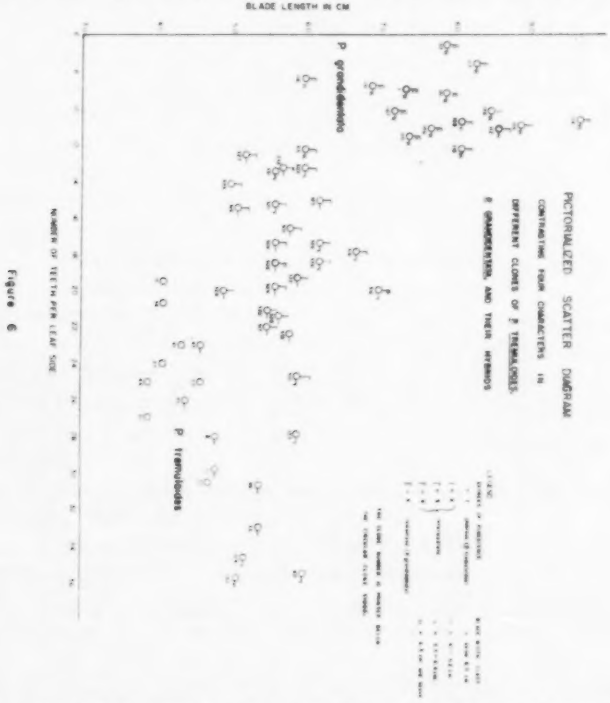


Figure 6

FIG. 6. Pictorialized scatter diagram, contrasting four characters in different clones of *P. tremuloides*, *P. grandidentata*, and their hybrids.

ered on several catkins. Peto (1938) reported that one of the three hybrids near Ottawa, Canada, was "monoecious." An interesting phenomenon observed on one of the catkins from the predominately male hybrid was a row of female flowers proceeding from the base to the tip along one side of the catkin.

The bracts of the aments in the hybrid are characterized by digits that are not as deeply cleft as in *P. tremuloides*, but not as shallow as in *P. alba*. The stigma color of the hybrid (pink) is intermediate between that of its parents. The receptive stigma of *P. tremuloides* is typically red or scarlet, whereas that of *P. alba* is "yellow-green to rose" (Amann, 1956).

POPULUS ALBA × GRANDIDENTATA

One clone of the *alba* × *grandidentata* hybrid was discovered in Section 17, T. 10 N., R. 6 E., Saginaw County. This clone consisted of about 10 to 15 ramets, the largest of which was about 8 inches in diameter at breast height. Victorin (1935) was probably the first to recognize that *P. alba* was hybridizing with the native aspens of Quebec. Heimburger (1936) stated that the *P. alba* × *grandidentata* hybrid was probably the one that Victorin had observed, since the parents flower approximately at the same time. Heimburger (1936) discovered several hybrid trees, and Peto (1938) listed what were apparently seven different clones of this hybrid from Ontario and Quebec. McComb and Hansen (1954) reported two hybrid clones from southeastern Iowa, which were described by Little, Brinkman, and McComb (1957). Subsequently Gatherum (1960) has reported two additional clones from Iowa.

SUMMARY

Thirty-eight clones of the *P. grandidentata* × *tremuloides* hybrid are reported from 10 counties in the Lower Peninsula of Michigan. Although the majority of hybrids have leaf and bud characteristics intermediate between the two parents, three clones are suspected of being introgressants. The reasons for the abundance of hybrids and the greater frequency of hybrid clones in southeastern Michigan than in the northern part of the Lower Peninsula are discussed.

Two clones of the *P. alba* × *tremuloides* hybrid and one clone of the *P. alba* × *grandidentata* hybrid are reported and described.

APPENDIX

Location of *P. grandidentata* × *tremuloides* clones in the Lower Peninsula of Michigan

Clone number	Number of trees in clone	Location
301	5	Section 17, T. 10 N., R. 6 E., Saginaw County
302	13	NW1/4, SE1/4, Section 25, T. 37 N., R. 4 W., Emmet County
303	3	SE1/4, SW1/4, Section 25, T. 37 N., R. 4 W., Emmet County
304	2	Section 6, T. 7 S., R. 7 E., Monroe County
305	2	Section 6, T. 7 S., R. 7 E., Monroe County
306	1	Section 6, T. 7 S., R. 7 E., Monroe County
307	2	Section 6, T. 7 S., R. 7 E., Monroe County
308	4	Section 6, T. 7 S., R. 7 E., Monroe County
309	3	Section 6, T. 7 S., R. 7 E., Monroe County
310	1	Section 6, T. 7 S., R. 7 E., Monroe County
311	1	Section 6, T. 7 S., R. 7 E., Monroe County
312	3	Section 6, T. 7 S., R. 7 E., Monroe County
313	8	NE1/4, Section 33, T. 10 N., R. 5 E., Saginaw County
314	6	S1/2, SE1/4, Section 23, T. 4 S., R. 7 E., Washtenaw County
315	6	S1/2, SE1/4, Section 23, T. 4 S., R. 7 E., Washtenaw County
316	ca. 50	N1/2, NW1/4, Section 28, T. 4 S., R. 8 E., Wayne County
317	ca. 20	N1/2, NW1/4, Section 28, T. 4 S., R. 8 E., Wayne County
318	3	N1/2, NE1/4, Section 30, T. 4 S., R. 8 E., Wayne County
319	1	N1/2, NE1/4, Section 30, T. 4 S., R. 8 E., Wayne County
320	ca. 30	Section 5, T. 8 N., R. 7 E., Genesee County
321	ca. 12	Section 5, T. 8 N., R. 7 E., Genesee County
322	2	SE1/4, Section 17, T. 9 N., R. 7 E., Genesee County
323	3	SE1/4, Section 17, T. 9 N., R. 7 E., Genesee County
324	1	SE1/4, NW1/4, Section 19, T. 7 S., R. 6 E., Monroe County

Clone number	Number of trees in clone	Location
325	1	SE1/4, NW1/4, Section 19, T. 7 S., R. 6 E., Monroe County
326	1	E1/2, SW1/4, Section 24, T. 7 S., R. 5 E., Lenawee County
327	1	E1/2, SW1/4, Section 24, T. 7 S., R. 5 E., Lenawee County
328	1	E1/2, SW1/4, Section 24, T. 7 S., R. 5 E., Lenawee County
329	ca. 50	E1/2, SW1/4, Section 24, T. 7 S., R. 5 E., Lenawee County
330	1	NW1/4, Section 30, T. 6 S., R. 7 E., Monroe County
331	2	SE1/4, NE1/4, Section 33, T. 3 S., R. 9 E., Wayne County
332	6	SE1/4, NE1/4, Section 33, T. 3 S., R. 9 E., Wayne County
333	1	SE1/4, NE1/4, Section 33, T. 3 S., R. 9 E., Wayne County
334	Not recorded	Cedar Lake, Waterloo Recreation Area, near camp, Washtenaw County. (Wagner s.n.)
335	Not recorded	East side Jefferson Rd., Section 15, T. 16 N., R. 2 E., Midland County. (Wagner 8993)
336	Not recorded	Edge of Muskegon State Park, SW1/4, Section 16, T. 10 N., R. 17 W., Muskegon County. (Wagner 9250)
337	Not recorded	North side Water-Munith Rd., Section 15, T. 1 S., R. 2 E., Jackson County. (Wagner 9259)
338	Not recorded	M-83, 4.7 mi. south of Frankenmuth, T. 10 N., R. 6 E., Section 22, Saginaw County. (Wagner 9285)

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A DISJUNCT COMMUNITY OF CHESTNUT OAK IN MISSISSIPPI

EDWARD G. ROBERTS

Coker and Totten (1944) and Harrar and Harrar (1946) report the range of chestnut oak (rock oak, rock chestnut oak), *Quercus prinus* L. as being south to Georgia and Alabama. The range map of Munns (1938) shows it in the northeastern tip of Mississippi — Tishomingo County. Mattoon and Beal (1936) report "It is found in the extreme northeastern counties, where it is common on the sandstone bluffs." Lowe (1913) writes of the vegetation of the North-Central Plateau of Mississippi that the typical upland for-

ests of the more sandy eastern parts of the region contain, among other things, *Quercus prinus*. This geographic description would include the western part of Calhoun County. But then Lowe goes on to report chestnut oak as being present in the bottoms of the same region and in the hills and bottoms of the deep loessal soils region to the west. There is unquestionably some confusion between *Quercus prinus* and *Quercus michauxii*. In a later bulletin, Lowe (1921) reports that chestnut oak is found in the northern part of the Pontotoc Ridge and, elsewhere in the bulletin, in the high hills about the headwaters of the Hatchie River. These seem to be two descriptions for essentially the same area. Further on in the bulletin he gives the range of chestnut oak as Tishomingo County and the high, rocky divides of Itawamba, Alcorn, and Tippah Counties. Itawamba is immediately to the south of Tishomingo. Alcorn and Tippah are immediately to the west and are at the headwaters of the Hatchie.

Recently, Newton Hanson of Bruce, Mississippi, forester for the E. L. Bruce Company, took the writer to see some chestnut oak in northwestern Calhoun County, Mississippi. One tree by the side of the road is over 16 inches d.b.h. It is in every respect a typical chestnut oak. Several others are within a few hundred feet of it. Mr. Hanson says that they are scattered over perhaps a thousand acres on a ridge which runs roughly north and south. Superficially, at any rate, there seems to be nothing to distinguish this ridge from countless others in north Mississippi. The area where the trees were seen is about three-quarters of a mile east of the Yalobusha County line and about three and one quarter miles south of the Lafayette County line in Section 22, Township 11 South, Range 3 West from the Chickasaw Base Line and Chickasaw Meridian or at Latitude 34° 7′ N, Longitude 89° 30′ W. This location is some eighty miles southwest of the range shown by Munns and perhaps sixty miles south and west of the locations reported by Lowe (1921).

The day may not be far distant when man converts this oak-hickory ridge to loblolly pine with the elimination of this disjunct chestnut oak community. — FORESTRY SCHOOL, MISSISSIPPI STATE UNIVERSITY.

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IMPORTANT NOTICE

to members, subscribers and librarians

Beginning with Volume 64 to be published in 1962, **Rhodora** will become a quarterly journal. It is anticipated that Volume 64 and subsequent volumes will contain approximately the same number of pages as previously published recent volumes. It will be the aim of the editors to have each quarterly number consist of 96 pages, including the cover. The above change does not imply any other changes in editorial policy.

The Editors

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